Fundamental concepts of population ecology and disease propagation dynamics rely heavily on the basic notions coming from the general qualitative theory of differential equations. For example, in the book *The Ecology of Wildlife Diseases* we may find such terms as *equilibrium population* that must be perturbed to estimate certain parameter values (p. 45), *reproduction number* (p. 48), *structural stability/instability* of a model (p. 50), *bifurcation theory* (p. 61), *stability analysis* for the equilibrium (steady) states (p. 69), *Law of Mass Action* (p. 87), etc.

We will discuss (in simple terms) the underlying ideas related to these notions.

**Main goal of this part of the course:** teach you how to read articles with models formulated in terms of differential (and difference) equations; also, teach you how to derive and analyze the models formulated in terms of differential equations.
1. **Introduction.** Where do the models come from? What is the relation between the statistics and the dynamic models? When the data is collected, which curves do we want to fit to the data and why?

In what follows we will use notation $t$ for independent variable (time), and notation $u$ for dependent variable (concentration, population density, etc.)
2. Assume that the parameters are known exactly (in reality, they must be estimated from the experimental data). We want to know what types of behavior (qualitative and quantitative) to expect. It is convenient to associate numerical values with such quantities as birth/death rate coefficients, mobility, etc., to compare the characteristics of healthy and infected individuals.

3. Derivation of the elementary model:

Simplistically,

\[ \Delta u = u(t + \Delta t) - u(t) \approx ku(t^*)\Delta t, \]

where

\[ t^* \in [t, t + \Delta t], \quad k = \text{(birth rate coef - death rate coef)}. \]

Divide by \( \Delta t \) and take the limit as \( \Delta t \to 0 \):

\[ \lim_{\Delta t \to 0} \frac{\Delta u}{\Delta t} = \frac{du}{dt} = k \lim_{\Delta t \to 0} u(t^*). \]

Thus,

\[ \frac{du}{dt} = ku(t). \]

Initial condition must be specified:

\[ u(0) = u_0. \]

Solution can be easily guessed: we recall that

\[ \frac{de^{kt}}{dt} = ke^{kt}. \]

The equation can be multiplied by any nonzero constant! Thus, the general solution of this linear homogeneous equation is

\[ u(t) = Ce^{kt}, \]
where $C$ is an arbitrary constant of integration.

Finally, substituting the general solution into the initial condition, we define $C$:

$$u(0) = C = u_0, \quad \text{so,} \quad u(t) = u_0 e^{kt}.$$ 

Here are some characteristic shapes of $u(t)$ for various $u_0$:

4. Phase line. Phase line is the $u$-axis. Analysis of solution behavior on the phase line (and later, in the case of several dependent functions, on the phase plane) is a powerful tool that allows one to make conclusions on the qualitative behavior of the solution (e.g., whether the population is increasing/decreasing, going to a steady state, etc).

We recall that the derivative $du/dt$ represents the rate of change: if $du/dt > 0$, then the function $u$ is increasing; if $du/dt < 0$, then the function $u$ is decreasing.

In the phase line we show the increase (decrease) of $u$ for increasing $t$ by the arrow pointing to the right (left):

For the equation

$$\frac{du}{dt} = ku(t)$$

the phase line may be constructed as follows:
In general, we have
\[ \frac{du}{dt} = f(u), \]
and

For steady states \( u = \bar{u} = \text{const} \) we have \( d\bar{u}/dt = 0 \), and thus \( f(\bar{u}) = 0 \). From this equation we find \( \bar{u}_1, \bar{u}_2, \text{etc.} \)
5. Stability of the steady states. Geometric considerations; domains of attraction.

Thus, we conclude that
if $f'(\bar{u}_i) > 0$, then $\bar{u}_i$ is unstable;
if $f'(\bar{u}_i) < 0$, then $\bar{u}_i$ is stable;
if $f'(\bar{u}_i) = 0$, then further analysis is needed:

6. Linearization. Analytically the same results may be obtained as follows.

Let the system have a steady state $u_i$. We introduce a small perturbation (e.g., we add a small number of species to the system, or remove a small number of species). What is going to happen to the population?
We substitute \( u(t) = \bar{u}_i + \alpha(t) \) \((|\alpha(0)| \ll 1)\) into the equation \( du/dt = f(u) \). Since \( d\bar{u}_i/dt \equiv 0 \), we have:

\[
\frac{d\alpha}{dt} = f(\bar{u}_i + \alpha(t)).
\]

Taylor series expansion with the center at \( \bar{u}_i \):

\[
f(\bar{u}_i + \alpha) = f(\bar{u}_i) + f'(\bar{u}_i)\alpha + \frac{f''(\bar{u}_i)}{2!}\alpha^2 + \ldots.
\]

At the steady state \( f(\bar{u}_i) = 0 \). Then, for \( \alpha \) “small”, we arrive at the linear equation that we already know how to solve:

\[
\frac{d\alpha}{dt} = f'(\bar{u}_i)\alpha, \quad \alpha(0) = \alpha_0 \text{ given}.
\]

We write:

\[
\alpha(t) = \alpha_0 e^{f'(\bar{u}_i)t},
\]

and so

- if \( f'(\bar{u}_i) > 0 \), then \( \bar{u}_i \) is unstable;
- if \( f'(\bar{u}_i) < 0 \), then \( \bar{u}_i \) is stable;
- if \( f'(\bar{u}_i) = 0 \), then further analysis is needed: higher order terms in the Taylor series expansion must be considered.

7. **Bifurcations.** Usually models contain parameters. Let us change some parameter and consider solutions of the models for different parameter values. Bifurcation is the abrupt change of the qualitative behavior of model solutions (e.g., change in the number of steady states, change in the stability properties of steady states, etc.) for certain, so-called, bifurcation values of the parameter. (Parameter itself then is often called the bifurcation parameter.)

Consider a function \( f(u, \lambda) \), where lambda is a parameter.
Geometry of the bifurcation ($\lambda = \lambda^*$ is the bifurcation value of the parameter):

8. Bifurcation diagram.
9. **Logistic equation.** “Heuristic” derivation:

Population growth/decay coefficient is population dependent.

The simplest form of population dependent growth rate coefficient that decays as population increases is

\[ k(u) = K \times \left(1 - \frac{u}{M}\right), \]

where \( M \) is called *carrying capacity*, and \( K = \text{const} \).

Then,

\[
\frac{du}{dt} = k(u(t))u(t) = Ku \left(1 - \frac{u}{M}\right)
\]

\[ = Ku - \beta u^2 = \text{growth w.o. competition} - \text{competition}. \]

Here \( \beta = K/M \).

Another way to derive: Consider a well stirred batch reactor (closed tank). Let \( u \) be the population density of bacteria in the tank, and \( c \) be the food concentration. Assume \( k = k(c) = \kappa c \), then we have a system of equations

\[
\frac{du}{dt} = \kappa cu, \quad \frac{dc}{dt} = -\alpha \kappa cu,
\]

where \( 1/\alpha \) is, so-called, yield factor. Initial conditions are

\[ u(0) = u_0, \quad c(0) = c_0. \]

The above system can be reduced to one logistic equation as follows. Let us multiply the first equation by \( \alpha \) and add the two equations. We obtain,

\[
\alpha \frac{du}{dt} + \frac{dc}{dt} = \frac{d(\alpha u + c)}{dt} = 0.
\]

Integrating this equation, we get for any \( t \):

\[ \alpha u(t) + c(t) = \text{const}, \]

and from the initial conditions:
\[ \alpha u(t) + c(t) = \alpha u_0 + c_0 \quad \text{(conservation of mass!)} \]

From the above we express

\[ c(t) = \alpha u_0 + c_0 - \alpha u(t) = A - \alpha u, \]

substitute in the original equation for \( u \), to arrive at the logistic equation:

\[ \frac{du}{dt} = \kappa cu = \frac{du}{dt} = \kappa u(A - \alpha u) = Ku \left(1 - \frac{u}{M}\right), \]

where \( K = \kappa A \) and \( M = A/\alpha \).

**Phase line analysis of the logistic equation.**

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**Exact solution (derivation later!) of**

\[ \frac{du}{dt} = Ku \left(1 - \frac{u}{M}\right), \quad u(0) = u_0 > 0 \]

is

\[ u(t) = \frac{Mu_0}{u_0 + (M - u_0) \exp(-Kt)}. \]
10. **Logistic equation with harvesting.** Several ways to harvest! For constant rate of species removal (vs. constant effort):

\[
\frac{du}{dt} = Ku \left(1 - \frac{u}{M}\right) - h,
\]

where \( h \) is the harvesting term (bifurcation parameter).

For which value of \( h = h^* \) will the species go extinct?

\[
h^* = \max_{u \in [0,M]} Ku \left(1 - \frac{u}{M}\right) = K \frac{M}{2} \frac{1}{2} = \frac{KM}{4}.
\]

11. **Bifurcation diagram.**
12. Other useful facts.

(a) Non-dimensionalization/re-scaling. How many parameters are actually important?

\[
\text{dimensional variable} = \text{non-dimensional variable} \times \text{dimensional constant}
\]

**Example 1.** Consider

\[
\frac{du}{dt} = ku, \quad u(0) = u_0.
\]

Let \( u = U \times a, \; t = \tau \times b \), where \( a, b = \text{const} \), and \( U, \tau \) are non-dimensional variables. Substituting into the equation and condition, we obtain:

\[
\frac{a}{b} \frac{dU}{d\tau} = kaU, \quad aU(0) = u_0.
\]

If we choose

\[
a = u_0 \quad \text{(i.e., we measure } u \text{ in the units of } u_0), \quad b = 1/k,
\]

we can write:

\[
\frac{dU}{d\tau} = U, \quad U(0) = 1.
\]

NO PARAMETERS! After solving the above problem, we may return to the original variables by back substitution:

\[
U(\tau) = e^\tau, \quad \text{or} \quad \frac{u(t)}{a} = e^{t/b}, \quad \text{or} \quad u(t) = u_0 e^{kt}.
\]

**Example 2.** It can be easily checked that for the logistic equation problem the change to non-dimensional variables

\[
U = \frac{u}{M}, \quad \tau = Kt
\]

converts

\[
\frac{du}{dt} = Ku \left(1 - \frac{u}{M}\right), \quad u(0) = u_0,
\]

to

\[
\frac{dU}{d\tau} = U(1 - U), \quad U(0) = U_0 = \frac{u_0}{M}.
\]
(b) **Superposition principle.** What if we want to solve the non-homogeneous linear equation (i.e., equation that also contains terms without \( u \) or \( du/dt \)?)

**Example 3.** Consider

\[
\frac{du}{dt} = ku - h, \quad u(0) = u_0,
\]

where \( k, h, u_0 \) are constants.

Superposition principle: general solution of the non-homogeneous equation = general solution of corresponding homogeneous equation + particular solution of the non-homogeneous equation.

In our case the general solution \( u_G(t) \) of corresponding homogeneous equation, \( du/dt = ku \), is \( u_G(t) = C \exp(kt) \), where \( C \) is an arbitrary constant of integration. A particular solution \( u_P \) of the non-homogeneous equation may be sought in the form \( u_P = A = \text{const} \) (yet unknown). Substituting \( u_P \) into the original equation, we obtain:

\[
\frac{dA}{dt} = 0 = kA - h, \quad \text{and thus}, \quad A = \frac{h}{k}.
\]

Finally, we have

\[
u(t) = u_G(t) + u_P(t) = Ce^{kt} + \frac{h}{k},
\]

and, taking into account the initial condition,

\[
u(0) = C + \frac{h}{k} = u_0, \quad \text{and thus}, \quad C = u_0 - \frac{h}{k},
\]

we arrive at

\[
u(t) = u_0 e^{kt} + \frac{h}{k}(1 - e^{kt}).
\]

(c) **Solution of the logistic equation.** Consider a problem for the non-dimensionalized logistic equation:

\[
\frac{dU}{d\tau} = U(1 - U), \quad U(0) = U_0 > 0.
\]

Let us divide both sides of the equation by \( U^2 \):

\[
\frac{1}{U} \frac{dU}{d\tau} = \frac{1}{U} - 1.
\]
Next, we use the new variable $Z = 1/U$ and take into account that $dZ/dt = -(1/U^2)dU/dt$. The equation will now have the form:

$$\frac{dZ}{d\tau} = -Z + 1.$$ 

This is a linear non-homogeneous equation! Applying the procedure described earlier, we arrive at the general solution in the form:

$$Z = Ce^{-\tau} + 1,$$

or

$$U = \frac{1}{Z} = \frac{1}{Ce^{-\tau} + 1}.$$ 

Substituting this into the initial condition, we determine $C = (1 - U_0)/U_0$. Finally,

$$U(\tau) = \frac{U_0}{U_0 + (1 - U_0)\exp(-\tau)}.$$ 

Returning to the dimensional variables, we get the solution in the form presented earlier in the section on logistic equation.

**d) Time dependent growth rate constant.** The environmental conditions usually change in time influencing the birth and death rates. (The time scales of the processes are important!)

Consider

$$\frac{du}{dt} = k(t)u, \quad u(0) = u_0.$$ 

It can be shown that

$$u(t) = u_0 \exp \left( \int_0^t k(s)ds \right).$$
Example 4. If

\[ \frac{du}{dt} = \cos(t)u, \quad u(0) = u_0, \]

then we have an oscillating population:

\[ u(t) = u_0 e^{\sin(t)}. \]